
TWO NEW GENERA OF NEOTROPICAL LAURACEAE AND CRITICAL REMARKS ON THE GENERIC DELIMITATION¹

Jens G. Rohwer,² Hans Georg Richter,³
and Henk van der Werff⁴

ABSTRACT

Two genera, *Chlorocardium* and *Paraia*, are described, illustrated, and discussed. *Chlorocardium* includes two species previously placed in *Ocotea* and is known from Guyana and Surinam (*C. rodiei*), and Ecuador (*C. venenosum*). *Paraia* includes one species, *P. bracteata*, from the States of Pará and Amazonas, Brazil. Problems with generic placement of several other species are discussed. The usefulness of two-celled vs. four-celled stamens as a character to define genera is discussed, and examples of polyphyletic genera based solely on the two-celled condition are given.

The genera of the Lauraceae, with very few exceptions, are circumscribed by a combination of characters rather than by single exclusive characters. However, Kostermans (1957) noted that "Apparently the combination of characters is more or less indefinite, and almost all combinations are represented." Although this statement must not be taken literally, because in strictly mathematical terms millions of combinations would be possible with the given characters, it does emphasize the reticulate variation within the family. Naturally, not all combinations are equally frequent. The more frequent combinations correspond to the larger genera, while rare combinations have been treated in two different ways. They either have been placed in a genus of their own (e.g., *Anaueria*, *Dicypellium*, *Phyllostemonodaphne*, *Urbanodendron*), or they have been included as aberrant species in one of the larger genera. In the present paper we describe two new genera based on rare combinations of characters, and we discuss some of the discordant elements in larger genera, as well as several cases of unsatisfactory generic delimitation.

The first of our new genera has the most unusual flower structure. Ironically, it is based on a species that normally would be considered to be among the better known Lauraceae.

Chlorocardium Rohwer, Richter & van der Werff, gen. nov. HOLOTYPE: *Chlorocardium rodiei* (Schomb.) Rohwer, Richter & van der Werff.

Ceteris Lauracearum generibus differt foliis oppositis, floribus exinvolucratis tetrameris vel plerumque irregularibus, staminibus 12–20, verticillis 3–5 dispositis, subaequalibus, omnibus quadrilocellatis latrorso-extrorsis, sessilibus, basi biglandulosis, ovario pubescente.

Chlorocardium rodiei (Schomb.) Rohwer, Richter & van der Werff, comb. nov. BASIONYM: *Nectandra rodiei* Schomb. in Hook., London J. Bot. 3: 616. 1844. TYPE: Guyana. 20–50 mi. inland, along the rivers Essequibo, Cuyuni, Demerara, Pomeroon, Berbice, *Schomburgk 1004* (holotype, K; isotypes, G, L; probable isotypes with no. 1703 in B, GZU).

Nectandra leucantha var. *rodiaei* (Schomb.) Griseb., Fl. Brit. W. I. 282. 1860.

Ocotea rodiei (Schomb.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 236. 1889.

Chlorocardium rodiei is a species of considerable economic importance. Its wood ("Greenheart," hence the name *Chlorocardium*) is among

¹ We thank the curators of F, INPA, and NY for the loan of specimens and/or for providing duplicates. L. E. Skog (US) provided additional flowers of *Chlorocardium rodiei*, J. Kallunki (NY) provided the wood sample of *Paraia bracteata*, and John Myers made the habit drawing of *Paraia bracteata*.

² Institut für Allgemeine Botanik, Ohnhorststrasse 18, D-2000 Hamburg 52, Federal Republic of Germany.

³ Institut für Holzbiologie und Holzschutz, Bundesforschungsanstalt für Forst- und Holzwirtschaft, Leuschnerstrasse 91, D-2050 Hamburg 80, Federal Republic of Germany.

⁴ Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

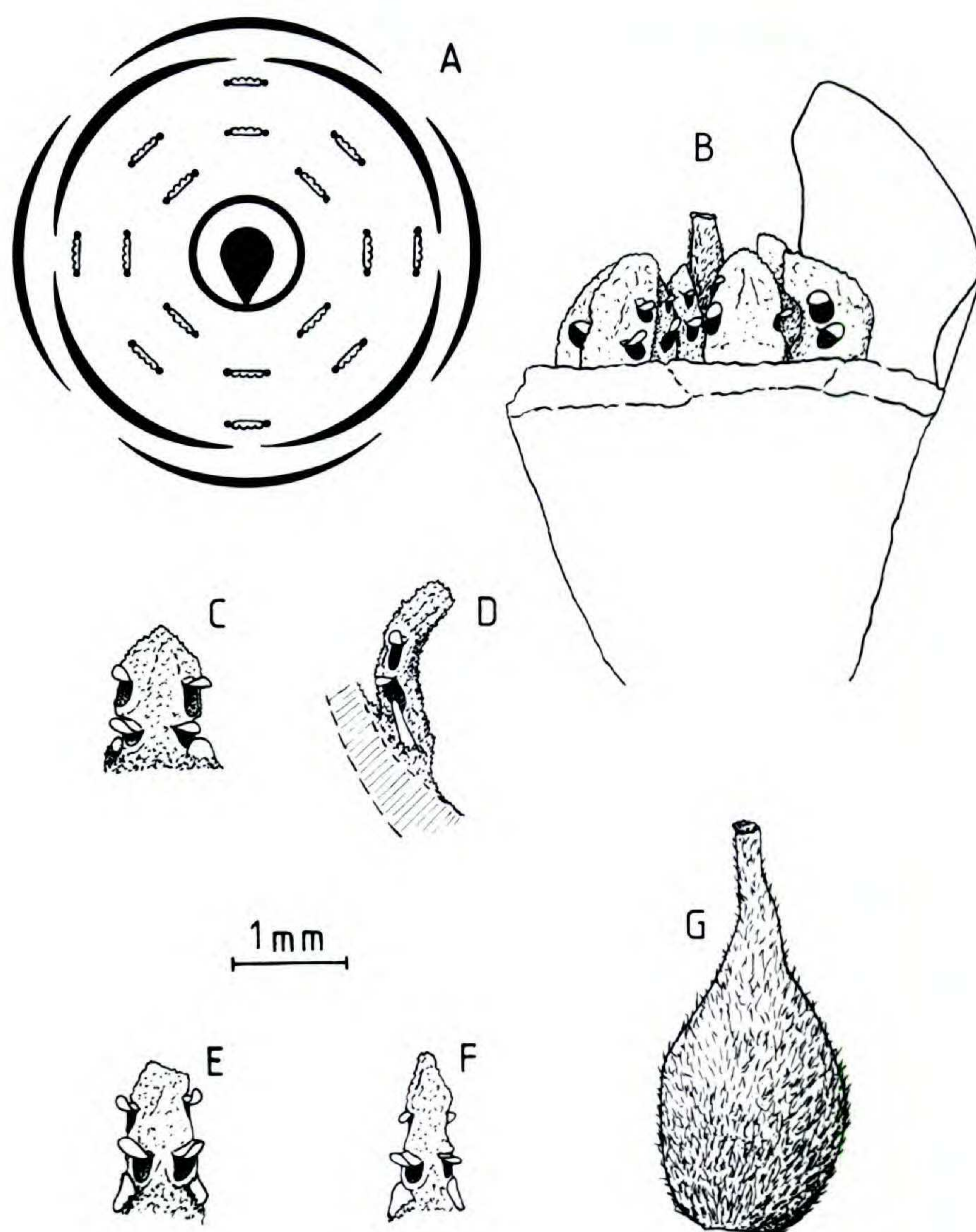


FIGURE 1. *Chlorocardium rodiei*. —A. Floral diagram of a regular flower with four whorls of stamens with four stamens each. —B. Flower, nearly all tepals removed. —C. Stamen of the first whorl, seen from outside. —D. Stamen of the first whorl, seen from side (note placement on the inside of the floral tube). —E. Stamen of the third whorl, seen from outside. —F. Stamen of the fourth whorl, seen from outside. —G. Ovary. Voucher: *Pipoly* 7530.

the most important commercial timbers in the family. Although the species has been known for more than 200 years, it is still poorly represented in the major herbaria, and very few flowering collections are known. This scarcity of flowers permitted a misinterpretation perpetuated until today. Schomburgk mentioned in the original description that most flowers appeared to be abnormal, with more than the usual number of parts. Similar statements can be found in all subsequent accounts on the species. Until today everyone who dissected a flower (including one of the authors) believed that he or she had picked a monstrosity when the flower turned out to be tetramerous or irregular, yet no one wanted to dissect a second flower because there was so little material.

As it turns out now, with more material available, the only regular flowers are indeed tetramerous (Fig. 1A), and irregular flowers are common in all specimens. Bentley & Trimen (1880) described

the flower as trimerous, with nine fertile stamens. We could not find this condition. Of the 14 flowers that we examined only one appeared to be trimorous, but it had 12 fertile stamens. Eight flowers were clearly tetramerous, of these we found:

- 1 with 4 tepals and 4 whorls of 4 stamens each
- 2 with 8 tepals and 3 whorls of 4 stamens each
- 3 with 8 tepals and 4 whorls of 4 stamens each
- 2 with 8 tepals and 5 whorls of 4 stamens each.

The remaining five flowers were irregular, usually with less than the full number of stamens in the inner whorls. One of the irregular flowers had only six tepals, and another had eight tepals but four whorls of five stamens each. Tepals with one or two apparently fully developed pollen sacs were found in both a regular and an irregular flower. The stamens (Fig. 1C–F) are almost equal, broadly sessile, and more or less tongue-shaped, each with two rather inconspicuous glands at the base and

with four locules, of which the upper ones are latrorse and the lower ones latrorse-extrorse. Toward the center of the flower the stamens become slightly smaller, and the inner whorls are inserted at successively lower levels within the floral tube. This configuration is reminiscent of the closely related Monimiaceae, but without parallel in the Lauraceae. It may be interesting to note that also the native name in Guyana is shared with a Monimiaceae. It is reported to be "Bebearu," "Bibiru," "Sipeira," "Sipiri," or "Sipiru"—undoubtedly the same root from which Aublet (1775) derived the name *Siparuna*.

Schomburgk reported that in times of food shortage the seeds of the Greenheart tree were used by the natives in a way similar to cassava, i.e., they were grated, and the starch was repeatedly washed to deprive it of the bitter alkaloids.

There is some uncertainty concerning the spelling of the specific epithet. The species is named for "Dr." Rodie, a Royal Navy physician who first described the medicinal uses of the plant. In the original publication the epithet is spelled "*rodioei*," with the *oe* printed as one character. Sandwith (1939) suggested that this was indistinguishable from *ae*, and that the correct spelling should be "*rodiaei*," because the name Rodie would be latinized as "Rodiaeus." However, from the following text of the description it is obvious that *oe* and *ae* are indeed different characters. Since the spelling with *oe* lacks any foundation, we suggest that [in accordance with Art. 73.10. of the *Code* (Greuter, 1988)] it should be corrected to "*rodiei*," as has been done by Mez (1889) and most subsequent authors.

The second species of the genus *Chlorocardium* is poorly known:

Chlorocardium venenosum (Kosterm. & Pinkley) Rohwer, Richter & van der Werff, comb. nov. BASIONYM: *Ocotea venenosa* Kosterm. & Pinkley, Bot. Mus. Leaflet. Harvard Univ. 22: 241. 1969. TYPE: Colombia. Putumayo: Río Guamúes, Santa Rosa, alt. 1,060 ft., 77°05'W, 00°19'N, 26 Nov. 1966, Pinkley 555 (holotype, GH; isotypes, ECON, S, U).

In the original description of this species the authors state that "Most of the flower buds available for dissection were abnormal as a result of fungal attack." In fact, they are so few and immature on the type specimen that it does not look worthwhile to dissect any of them. The general aspect of the plant agrees very well with *Chlorocardium rodiei*, and the wood structure described

leaves no doubt that the two species are extremely close. *Chlorocardium venenosum* is known only from the border region of Colombia and Ecuador, while we have seen material of *Chlorocardium rodiei* only from Guyana. It also occurs in Surinam, but reports of a much wider distribution (as in Mell & Brush, 1913) appear to have no foundation.

The structure of the secondary xylem of the two species described here under *Chlorocardium* is highly unusual in two aspects: The interconnecting pit pairs between vessels as well as between vessels and parenchyma cells (rays and axial parenchyma) are extremely small (3–4 μm diam.), a condition absent not only from *Nectandra* and *Ocotea*, but from all Lauraceae with the exception of the small Asiatic genus of *Neocinnamomum*. More importantly, parenchyma cells are connected to adjacent vessels through unilaterally compound pitting with large, simple pits subtending two or more of the small bordered pits in the vessel elements. These large pits in the parenchyma cells are often traversed by branched or simple filiform protrusions of cell wall material. In addition, vessel elements in both species bear at the ends a partial or complete ring of large, windowlike pits that give the impression of a crown or corona, hence the term "coronated vessel elements" used by Kostermans et al. (1969) to describe this phenomenon quite unique in xylem anatomy.

The other aspect considered here is the complete lack of secretory cells in the secondary xylem. What might have been a chance observation for *Chlorocardium venenosum* described from only one specimen so far (Kostermans et al., 1969) becomes significant for *C. rodiei*: The countless descriptions dealing with the secondary xylem of this taxon have not once revealed the presence of secretory cells. Thus their absence, although generally not diagnostic in Lauraceae, might justly be used in conjunction with other characters to seriously question the traditional taxonomic affinities of these two species.

These findings are corroborated by the equally unusual structure of the secondary phloem of *C. rodiei* (for detailed description see Richter, 1981), which is characterized by special features different from the prevailing structural patterns in Lauraceae, among them the complete lack of secretory cells (sic).

Thus, the wood and bark structure supports a rather isolated position for *Chlorocardium*, but unlike the flower structure it does not suggest an affinity with the Monimiaceae.

Fruits of *Chlorocardium rodiei* have been described as large (6–7 cm long, 5 cm diam.) and

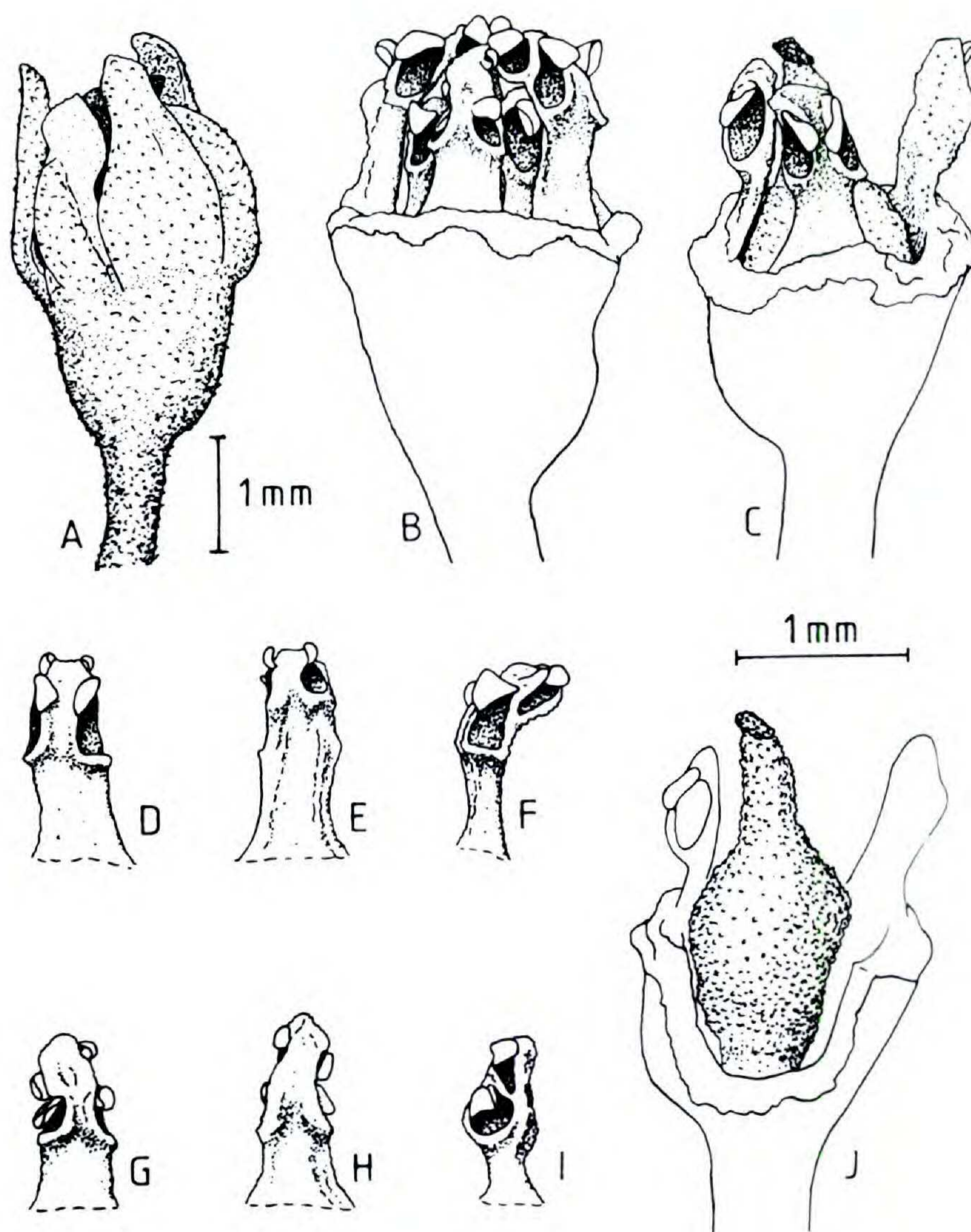


FIGURE 2. Undescribed new genus.—A. Flower.—B. Flower, tepals removed.—C. Receptacle with ovary, outer stamens removed.—D. Stamen of the first whorl, seen from outside.—E. Stamen of the first whorl, seen from inside.—F. Stamen of the first whorl, seen from side (curved inward).—G. Stamen of the second whorl, seen from outside.—H. Stamen of the second whorl, seen from inside.—I. Stamen of the second whorl, seen from side.—J. Ovary, its position in the receptacle schematically shown. Voucher: *Vásquez 6020*.

ellipsoid to ovoid-globose, seated in a shallow, single-margined cupule, 2–2.5 cm diam. (Mez, 1889; Kostermans, 1936). A recently collected specimen (*Pipoly 8616*, MO) shows a not very deep, lenticellate cupule, ca. 1.5 cm diam. and a clearly exserted, ovoid fruit, ca. 1.5 cm long. Fruits and cupule are attached to the twigs. The tree was still flowering at the time of collection, and it is possible that the fruits were immature. Fruits of *C. venenosum* were described as depressed-globose, 4.5 cm high and 5.5 cm diam., almost completely enclosed by the cupule. A recent collection with fallen fruits agrees very well with this description; the fruits are up to 6 cm high and 7 cm diam., the cupule largely encloses the fruit, leaving an orifice of about 2.5 cm diam. Fruits are used by the Kofan Indians to make arrow poison. The very large cupule of *C. venenosum* readily separates this species from *C. rodiei* with its much smaller,

shallow cupule. With the exception of the recently described *Ocotea megacarpa*, fruit size of the two *Chlorocardium* species far exceeds that of any *Ocotea* or *Nectandra* species.

Recently we found another species with opposite leaves and variable staminal configuration that in some characters resembles *Chlorocardium* but also shows marked differences (Fig. 2). Like in all other neotropical Lauraceae (except *Chlorocardium*) the flowers are trimerous, invariably with six tepals and not more than three whorls of fertile stamens. The fourth whorl, which in many Lauraceae is staminodial, seemed to be represented only in the fragments of one broken flower. In 25 reasonably intact flowers examined we found the following configurations:

10 flowers with whorl I and II 4-locular, whorl III 2-locular

- 8 flowers with whorl I and II 4-locular, whorl III absent
- 4 flowers with all three whorls 4-locular
- 2 flowers irregular

In the 2-locular stamens it is the upper pair of locules that is lost. The lower pair, like in *Chlorocardium*, is latrorse-extrorse in all stamens; the upper pair can be latrorse or latrorse-introrse. Like in *Pleurothyrium* the flaps open toward the abaxial side of the stamens. The outer stamens (especially whorl I, Fig. 2D–F) are bent inward, overarching the inner stamens. All stamens have distinct, broad filaments, and there is no trace of glands. The large ovary is inserted in a deep, cup-shaped receptacle. All parts of the flower, including the ovary and the inside of the receptacle, are covered with papillae.

This combination of characters is unique within the family, and we have no doubt that our material represents a new genus. However, as our observations are based on only one collection (*R. Vásquez 6020*), we postpone the formal description until more material becomes available.

The second new genus that we describe in this paper is far less unusual in its staminal configuration. Yet its combination of characters does not fit any of the known genera.

***Paraia* Rohwer, Richter & van der Werff, gen. nov.** HOLOTYPE: *Paraia bracteata* Rohwer, Richter & van der Werff.

Ceteris Lauracearum generibus differt foliis in apice ramulorum subverticillatim congestis, floribus subglobosis bracteis conspicuis plerumque numerosis subtentis, tepalis margine hyalinis interne epapillosis glabrisque, staminibus novem, antheris quadrilocellatis locellis arcuatim juxtapositis, ovario bene evoluto in tubo profundo, cupula duplicimarginata margine exteriori longiore et perianthii segmentis auctis sexlobato.

***Paraia bracteata* Rohwer, Richter & van der Werff, sp. nov.** TYPE: Brazil. Pará: Mun. Oriximiná, Rio Trombetas, right bank, Porto Trombetas, road to Mineração Rio Norte, km 60, beyond Bauxite mine, 29 Aug. 1980 (fl, fr), *Cid et al. 1890* (holotype, MO; isotypes, HBG, INPA 96058 not seen, NY). Figures 3, 4.

Frutex vel arbor ad 8 m (20 m?) alta. Ramuli teretes, hornotini gemmaeque dense ferrugineo tomentosi. Folia petiolis crassiusculis 5–13 mm longis canaliculatis, fere omnia apice ramulorum congesta, oblanceolata vel obovata vel oblonga, adulta 14–35 cm longa, 5–12.5 cm lata, apice ex acuto vel obtuso manifeste acuminata, basi cuneata vel rarius acuta (basi ipso interdum obtusa), in sicco ± olivacea, adulta supra opaca vel nitidula glabra, subtus peropaca subglabra, margine plano, nervis secundariis

utroque costae latere 6–11 e nervo medio sub angulo 40–80° prodientibus. Inflorescentiae e gemmae terminali squamarum axillis prodientes, anguste thyrsoides, quam folia multo breviores (3–11 cm longae, pedunculis 1.2–8 cm longis), dense ferrugineo-tomentosae. Flores breviter pedicellati vel subsessiles in apice inflorescentiae ramulorum ± glomerati, bracteis conspicuis subtenti, plerumque tubo receptaculi conspicuo. Perianthium flore plena subglobosum, haud patens, 2–3.5 mm diametro. Tepala suborbiculares, basi crassa, margine hyalino, externe basi et linea media tomento ferrugineo, interne epapillosa glabrae. Stamina novem, ca. 0.8–1.5 mm longa, epapillosa, quadrilocellata vel serie prima raro bilocellata, sex exteriora eglandulosa filamentis gracilibus locellis subapicalibus arcuatim vel linea unica juxtapositis, tria interiora basi biglandulosa filamentis crassiusculis locellis subapicalilateralibus. Staminodia parva, subulata, dense tomentosa. Receptaculi tubus profundus, saltem longitudine staminum, angustus, intus dense tomentosus. Pistillum glabrum, elongatum, ca. 2–2.4 mm longum, stylo ovarium aequante vel eo paulo longiore. Cupula obconica vel subhemisphaerica, 12–15 mm diametro, 6–8 mm profunda, duplicimarginata, margine exteriori longiore et perianthii lobis incrassatis manifeste sexlobato. Bacca ellipsoidea vel plerumque ovoidea, ca. 14–24 mm longa et 10–12 mm diametro.

Shrub or small tree, usually to ca. 8 m tall (only *Silva 2220* from a tree 20 m tall). Twigs round, the youngest with a dense cover of long (ca. 0.4–1 mm long), straight to curled, ± erect, relatively thick, reddish brown hairs, quickly becoming felt-like, easily worn off. Terminal buds covered by relatively large (4–7 mm) scales, somewhat spreading, with the same kind of indument as the twigs on outside (though not always dense at the margins), glabrous on inside. Leaves drying with a characteristic grayish green to olive-brown color, alternate but with few exceptions clustered at the tip of the branchlets (sometimes a second, older whorl still present), 14–35 cm long, 5–12.5 cm wide, ca. 2.3–4(–4.5) times longer than wide, oblanceolate, obovate or oblong, widest in the middle or mostly slightly above, toward the apex acute to obtuse, the tip itself with a distinct acumen, base mostly long, ± cuneate or sometimes acute (at the very base occasionally abruptly obtuse), lateral veins 6–11 on each side of the midrib, diverging at 40–80°, midrib and secondaries above ± slightly impressed but the vein itself convex, below prominent, tertiary reticulation above almost invisible to impressed and slightly convex, below slightly raised to prominent. Indument of leaves consisting of the same kind of hairs as on the twigs, even in the youngest leaves above sparse, sometimes dense on midrib, below moderately sparse and highly unevenly distributed, often dense on midrib, or sometimes subglabrous from the beginning; mature leaves entirely glabrous or below often with rudiments of the indument. Inflorescences springing from the

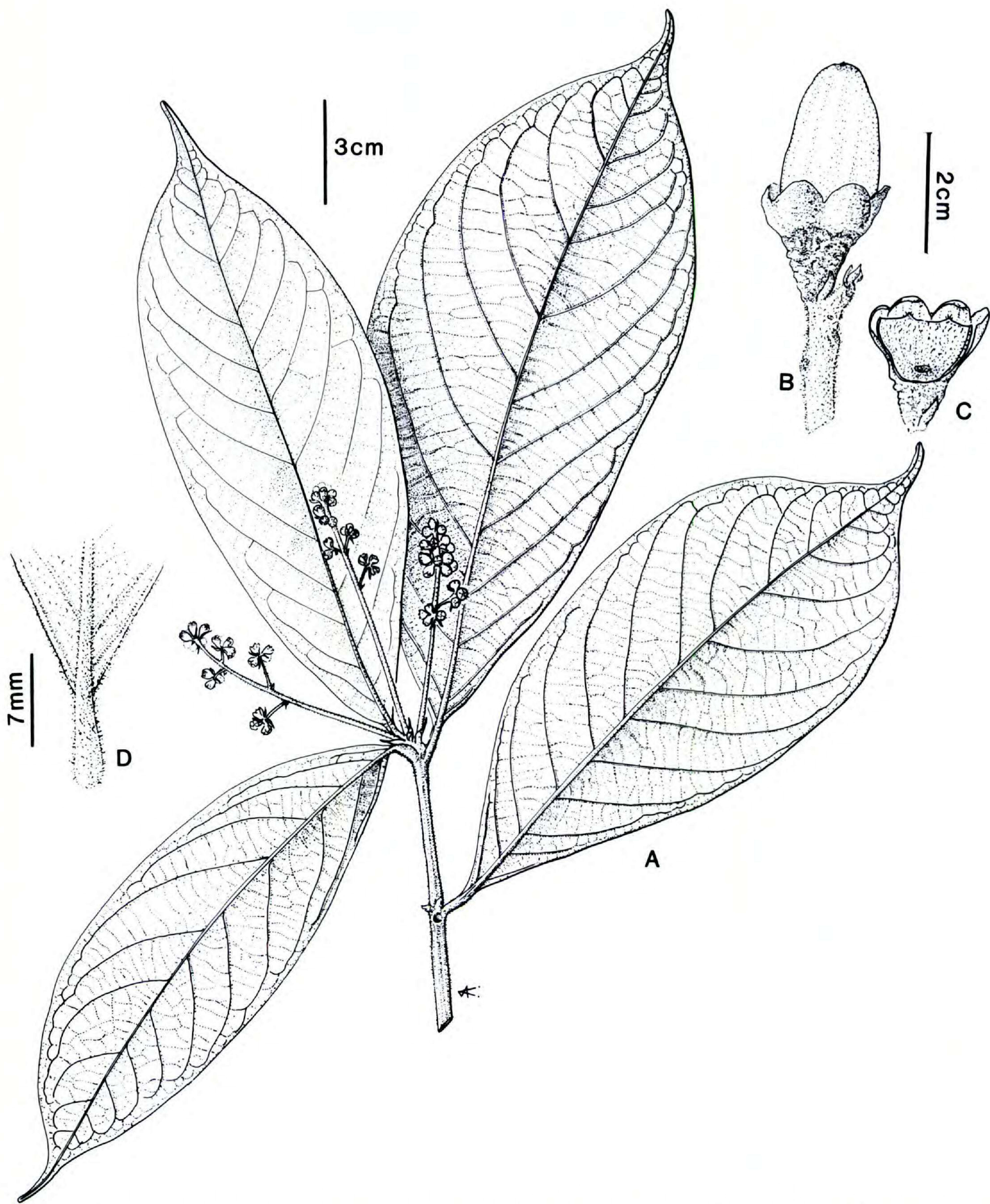


FIGURE 3. *Paraia bracteata*.—A. Habit.—B. Fruit.—C. Cupule, cut open, showing the double margin.—D. Detail of leaf base. Vouchers: A, D, *Cid 1890*; B, C, *A. S. Silva et al. 72*.

scales of the terminal bud, 2–8(–11) cm long with a peduncle of 1.5–5.5(–8) cm, narrowly thyrsoïd, the lateral branches not more than 1 cm long (at anthesis; often enlarged afterward). Flowers apparently bisexual (but see below), sessile or with a short pedicel (to 1 mm), clustered at the tip of the inflorescence branches, subtended by relatively large

bracts, which are often more numerous than the flowers but (at least partly) fall off during anthesis. Perianth subglobose, ca. 2–3.5 mm diam., opening only slightly during anthesis. Tepals 6, suborbicular, fleshy at the base, hyalinous toward the margins, only on the outside at the base and in the middle with reddish hairs, otherwise glabrous, with-

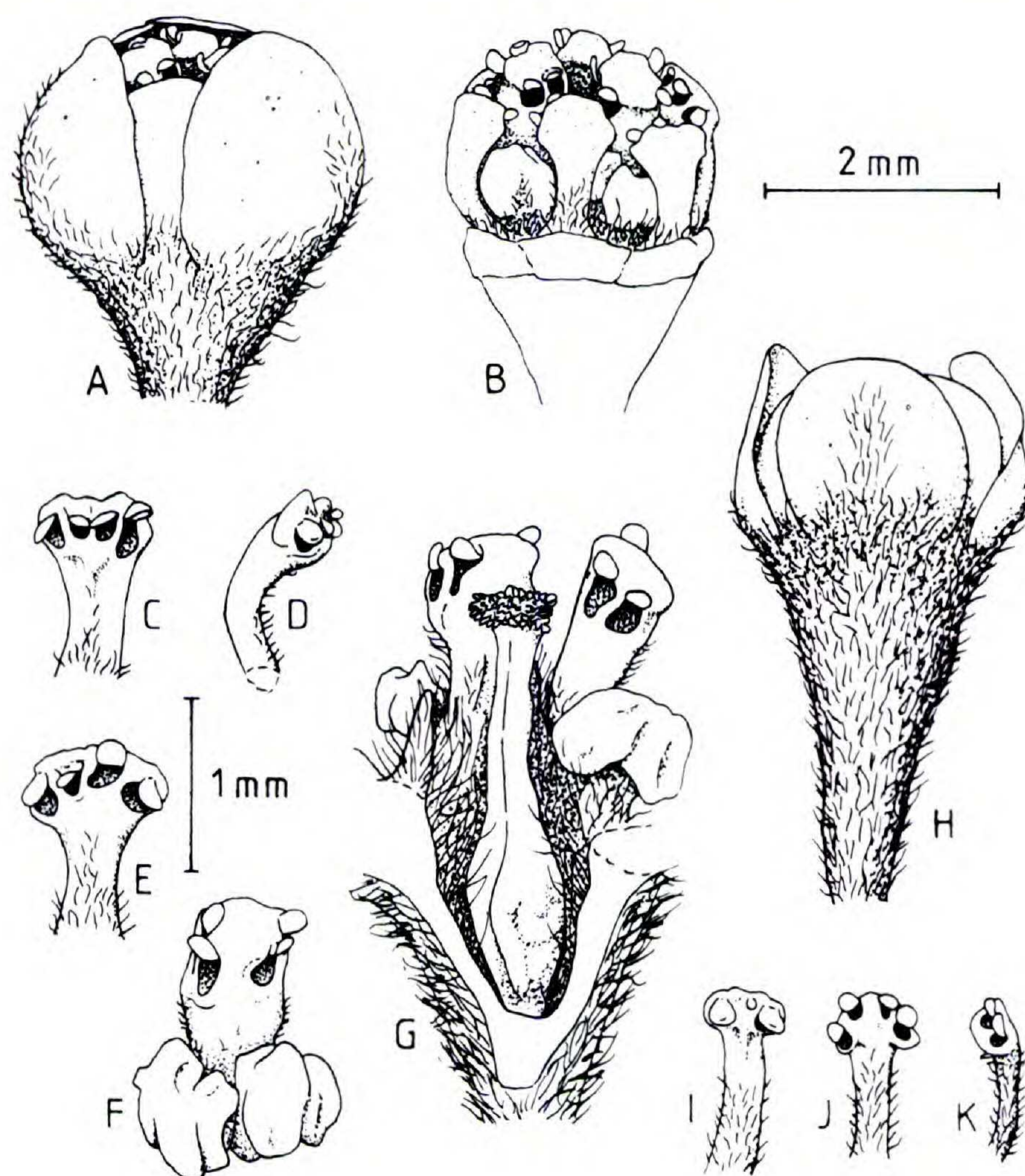


FIGURE 4. *Paraia bracteata*. —A. Flower, globular form. —B. Flower, tepals removed. —C. Stamen of the first whorl (of A), seen from inside. —D. Stamen of the first whorl, seen from side. —E. Stamen of the second whorl, seen from inside. —F. Stamen of the third whorl, seen from outside. —G. Receptacle with ovary, staminode and two inner stamens, cut open, tepals and outer stamens removed. —H. Flower, elongate form. —I. Stamen of the first whorl (of H), 2-locular form, with a rudimentary third locule, seen from inside. —J. Stamen of the second whorl, seen from inside. —K. Stamen of the second whorl, seen from side. Vouchers: A–G, *Cid* 1890; H–K, *Ducke* s.n.

out any papillae. Stamens 9, 4-thealous or in the first whorl rarely 2-thealous, without papillae, the outer six 0.8–1.4 mm long, their slender filaments 0.5–0.8 mm long, at least at the base and on adaxial side with some hairs, the anthers wider than long, thecae subapical, introrse, arranged in an arc or (especially in the first whorl) almost in a horizontal line, the inner three stamens 0.8–1.6 mm long, their filaments thick, only slightly narrower than the anther, 0.4–0.8 mm long, at least laterally hairy, each with a pair of conspicuous glands at its base, the thecae subapical in two \pm lateral pairs, almost at the same level (the adaxial ones slightly higher than the abaxial ones). Staminodia three, 0.3–0.6 mm long, subulate, very hairy. Receptacular tube 1.2–2 mm deep, narrow, densely hairy inside. Pistil slender, ca. 2–3.4 mm long, style as long as the ovary or slightly longer. Cupule broadly obconical to subhemispherical, 12–15 mm diam., 6–8 mm deep, distinctly double-rimmed, the outer margin longer, crowned by enlarged te-

pals (which, however, seem to break off easily). Berry ellipsoid to ovoid, 14–24 mm long, 10–12 mm diam., often with truncate tip.

Additional specimens examined. BRAZIL. AMAZONAS: Manaus–Itacoatiara Highway, Colonia Santo Antonio, 27 Oct. 1966 (fr), *Allen & L. Coêlho* 330 (HGB, NY); Rio Cuieiras–Manaus trail, km 1, 6 Apr. 1974 (fl), *Campbell et al.* in *Prance* 21901 (HGB, MO, NY); Manaus, Estrada de Flores (Rosa de Maio), Feb. 1974 (st), *D. Coêlho* s.n. (HGB, INPA 46534), near Igarapé Mindú, 12 July 1929 (fl), *Ducke* s.n. (U), along road to Aleixo, 12 Aug.–1 Sep. 1936 (fr), *Krukoff* 7996 (F, NY); Rio Cuieiras, 2 km below mouth of Rio Brancinho, 11 Sep. 1973 (fl), *Prance et al.* 17749 (HGB, NY); Manaus, Igarapé do Bindá, 19 Oct. 1961 (fr), *Rodrigues & Chagas* 2666 \equiv 3466 (HGB, INPA 10016, NY); Manaus–Caracaraí road, km 19, 20 Sep. 1961 (fr), *Rodrigues & L. Coêlho* 3317 (NY). PARÁ: Belém, Instituto Agrônômico do Norte, 3 Aug. 1962 (fl juv.), *Allen* 79 (NY); Mun. Oriximiná, Rio Trombetas, left bank, at Lago Moura, 22 Aug. 1980 (fl), *Cid et al.* 1825 (HGB, MO); Lago Cuçari, Planalto de Santarém, area of forest inventory by IAN, SPVEA, and FAO, 15 Apr. 1955 (fl), *Fróes* 31668 (NY); Mocambo, EMBRAPA Forest Reserve, ca. 10 km from Belém, 13

Nov. 1984 (st), *Gentry 48956* (MO), 10 Oct. 1966 (fr), *Pires & N. T. Silva 10245* (HBG), 28 Sep. 1967 (fr imm.), *Pires & N. T. Silva 10947* (NY), 2 Sep. 1967 (fr), *Pires & N. T. Silva 10949* (NY), 3 Aug. 1973 (fl), *Pires 13219* (HBG, NY); Mun. Almerim, Estrada do Pedrão, km 40, 12 Nov. 1978 (fr), *Santos 284* (F); Serra dos Carajás, 13 km from AMZA headquarters, road to sawmill, 18 Oct. 1977 (fr), *A. S. Silva et al. 72* (HBG, MO); Santarém, Estrada do Palhão, km 35, near Igarapé Curupira camp, 24 Aug. 1969 (fr), *M. Silva & Souza 2402* (HBG, MO, NY); Rio Jarí, Monte Dourado, Planalto B., between Pilão and Repartimento, 28 Oct. 1968 (fr), *N. T. Silva 1328* (HBG, NY); Jarí, road from Bandeira to Pilão, km 39, 18 June 1969 (fl, fr imm.), *N. T. Silva 2220* (HBG, NY).

WOOD DESCRIPTION

The wood and bark descriptions are based on the type collection only. The specimen comes from a small tree ca. 7 m tall. The wood sample has an average diameter of 7 cm, covered by a grayish brown bark ca. 3 mm thick. Wood and bark are slightly aromatic.

General. Wood uniformly yellowish brown; heartwood probably dark brown as indicated by the presence of darker colored patches around a zone damaged by insect larvae; evenly textured, dense and heavy (specific gravity ca. 0.85/cm³).

Anatomy. Wood diffuse porous throughout, pores evenly distributed, thin-walled and angular in outline; solitary and radial multiples of 2–5 in variable proportions; largest pores 100–150 μ m diam., frequency 15–22/mm². Vessel perforations exclusively simple; intervacular pits invariably alternate, mostly circular in outline and not crowded, pit apertures included; pits 9–11 μ m diam. Tyloses common, thin-walled to sporadically sclerotic; no gum deposits observed. Fibers libriform, of medium wall thickness; regularly septate; generally ca. 15 μ m diam., rarely up to 20 μ m; pits very small and inconspicuous, mostly confined to radial walls; growth increments distinct microscopically, marked by 1–2-seriate tangential bands of wide-bodied fibers (up to 30 μ m diam.); no imperforate tracheary elements observed. Parenchyma basically paratracheal sparse to irregularly vasicentric; rather inconspicuous unless interspersed with large idoblasts (oil cells) as part of the vasicentric sheath; vertical strands composed of 4–6 individual cells; pits to vessels enlarged, oval to gashlike and extended horizontally. Wood rays predominantly biseriate, heterogeneous with 1–2, rarely up to 4, marginal rows of upright and/or square cells; height of largest rays 0.5–0.8 mm; vessel ray pits enlarged, oval to irregular or gashlike; reddish brown gum deposits sometimes present. Crystalline de-

posits and silica absent. Oil cells common, associated with axial and ray parenchyma; very large with diameters up to 70 μ m and axial extensions up to 0.35 mm (associated with marginal ray cells) and 0.70 mm (associated with parenchyma strands).

BARK DESCRIPTION

Secondary phloem ground tissue composed of conducting (sieve and companion) cells and phloem parenchyma. Interspersed are numerous oval or diamond-shaped, rarely tangentially extended sclereid islands consisting of vertically elongate, columnar sclereids. Secondary phloem fibers are absent. Toward the periphery the secondary phloem is delimited by a continuous ring of small, irregularly shaped and largely isodiametric sclereids enclosing few and widely spaced groups of primary phloem fibers. The sclereid ring is followed by cortical parenchyma gradually phasing into several rows of rectangular, radially oriented phelloderm cells (replete with dark colored gum deposits or sclerified) and a narrow (2–3 rows of similar but empty cells) terminal phellem. Just inside the sclereid ring few isolated radially flattened sclereids are present. Phloem rays resemble wood rays in dimensions and composition. Their radial course through the secondary phloem is ragged due to the spatial rearrangement of other constituents following the early collapse of conducting tissues. Ray cells become sclerified when traversing sclereid islands. Oil cells are scattered throughout the secondary phloem and the cortical parenchyma. Crystalline inclusions are deposited in ray and axial parenchyma in considerable quantities, usually as minute acicular crystals.

Note. The sclereid island constituents (columnar sclereids) are more or less rectangular in cross section, with the larger side extending in radial direction. The narrow tangential faces have pointed ends, thus resembling fibers in tangential view. The polylamellate structure of the cell wall, the distinct pit canals, and the type of lignification exposed by differential staining, however, betray their probably parenchyma-derived sclerenchymatic nature.

Paraia bracteata was first recognized as a new species by Beulah Coe-Teixeira. She annotated several specimens as *Nectandra paraensis* Coe-Teixeira, but she never published the name. While working toward a revision of the genus *Nectandra*, J. Rohwer found that this taxon has nothing in common with *Nectandra* except the technical character of “four locules of the anther arranged in an arc.” There are no other species of *Nectandra* with the leaves distinctly crowded at the tip

of the branchlets, with hyalinous tepals entirely lacking papillae, or with clearly double-rimmed cupules. Also, the general aspect of the plant, its flowers or flower parts, do not suggest *Nectandra*. Sterile material is often annotated as *Aniba*, which can be quite similar. Vegetatively and even in its inflorescences *Paraia bracteata* strikingly resembles *Rhodostemonodaphne miranda* (Sandw.) Rohwer, but this similarity does not extend to the inner organization of the flower. After discussing the possible relationships of this new species, we concluded that we would have to describe it as a new genus. For every known genus we could find at least three important reasons why it should not be included there.

Judged by its rather commonplace lauraceous wood structure alone, *Paraia bracteata* cannot be safely differentiated from all but a few neotropical Lauraceae, e.g., *Mezilaurus*, *Clinostemon*, *Caryodaphnopsis*. Nearly all positive and negative affirmative characters circumscribing the prevailing structural patterns of Lauraceae are present. In combination with the very specific bark structure, however, most neotropical genera of this family can be excluded as possible matches. Very good structural agreement can be found only in a small group of taxa comprising most species of *Aniba* and *Licaria*, and a few species currently ascribed to *Ocotea*. When taking into account the less diagnostic but nevertheless helpful general wood characters such as color and density, the scope can be narrowed down further to the few species constituting subg. *Canella* of *Licaria* (Kurz, 1982; Richter, 1985), and two strikingly similar species of *Aniba* (*A. canelilla* (HBK) Mez, *A. ferrea* Kubitzki). Even without supporting evidence from exomorphic characters, an attribution to the genus *Nectandra*, as initially proposed by Coe-Teixeira, can definitely be ruled out.

Following the traditional "number's game" of generic delimitation, it would seem that *Paraia* was not at all close to *Licaria*, which has only three fertile stamens (whorl III), each with two thecae. Only the double-rimmed cupule would fit that genus better than any other. However, when considering additional floral characters (which have received little attention up to now), a connection between *Paraia* and *Licaria* does not seem that far off. In *Licaria* it is quite common that the tepals are short and scarcely spreading at anthesis, and that only the style protrudes beyond the nearly globular perianth. Also the thickish, columnar stamens of the third whorl with their subapical thecae are somewhat similar to *Licaria*. The fact that the stamens of the first whorl are sometimes only

2-thecous in *Paraia* indicates a tendency toward reduction. If the thecae were entirely reduced in the outer whorls, the resulting staminodia would be quite similar to those of several *Licaria* species, with a slender filament and a flat, widened apex. Thus, the possibility that *Paraia* represents a more primitive offshoot of the line leading to *Licaria* cannot be ruled out.

When looked at individually, the flowers of *Paraia bracteata* appear to be invariably bisexual. However, when flowers from several different specimens are dissected, it seems that there are two types of flowers, differing in proportions. In the first type (Fig. 4A–G), the flowers are nearly globular, the receptacular tube not being apparent from the outside. The length of the stamens is approximately equivalent to the depth of the receptacle. In the second type (Fig. 4H–L) the stamens, although apparently fertile, are noticeably smaller. The receptacular tube is deeper, almost twice as long as the stamens, visible also from the outside. The ovary, however, is more or less the same size in both types. It is possible that the different proportions indicate an incipient separation of the sexes. It may, on the other hand, be just an expression of geographic differentiation. Such a differentiation is obvious in leaf shape: specimens from the surroundings of Manaus have relatively much narrower leaves than those from the state of Pará.

DISCUSSION OF GENERIC DELIMITATION IN THE LAURACEAE

OCOTEA RUBRA

A highly unusual combination of characters is also found in a species known as *Ocotea rubra* Mez. This species has more or less obovate, glabrous leaves, crowded at the tip of the branches. It therefore resembles *Mezilaurus* rather than *Ocotea* in its vegetative characters. The flowers, however, are unlike any other known species of Lauraceae. The tepals are shorter than the floral tube and usually more or less unequal, the outer ones smaller than the inner ones. The stamens are tongue-shaped and extremely papillose. Their four thecae are introrse and arranged in an arc on the stamens of the first and second whorl, but latrorse and in two pairs above each other in the third whorl. The staminodia of whorl four are almost as large as the inner stamens, but unlike very large staminodia in other genera they are not glandular. The ovary has a very slender style, as, e.g., in *Licaria* or *Mezilaurus*. The fruit is almost completely surrounded by a deep cupule during most

of its development, but about half exerted at maturity.

There is no other species of *Ocotea* with unequal tepals, and most of the other characters of *O. rubra* are very rare. Anatomical data (Richter, 1981) further underscore the isolated position of this species. Obviously, there is no reason to retain it in *Ocotea* other than reluctance to further increase the number of monotypic genera. In several characters (unequal tepals, broadly sessile stamens, reddish brown wood with very large cross-field and intervacular pits), *O. rubra* resembles the Asian genus *Nothaphoebe*, but the fruit is very different. *Nothaphoebe* does not have a well-developed cupule, but only a somewhat enlarged pedicel with the tepals persistent under the fruit.

TWO-LOCULAR VS. FOUR-LOCULAR ANTHERS

All of the taxa discussed above go beyond the current delimitation of the genera simply because they represent rare combinations of characters. They are therefore systematically isolated, but do not jeopardize the delimitation as such. There is, however, also an increasing number of cases that lead to serious doubts about the value of the current system. Traditionally, one of the most important characters used for the delimitation of genera is the number of thecae per anther, two vs. four. Although this character is indeed constant for the overwhelming majority of species within well-defined natural groups, its indiscriminate application may lead to artificial groupings.

Several neotropical species have the staminal configuration of one genus, yet they can be recognized as belonging to another genus based on all other characters. The current system is inconsistent in treating these species. Some are placed with their allies despite a staminal configuration that makes it impossible to key them out to the correct genus, whereas others are placed within the genus to which they would key out, regardless of their obvious affinity to species of a different genus. Thus, *Persea cuneata* Meissn., *P. bilocularis* Kopp, and *Caryodaphnopsis inaequalis* (A. C. Smith) van der Werff & Richter, e.g., have 2-thecous anthers, although their respective genera are defined by 4-thecous anthers, and *Beilschmiedia sulcata* (Ruíz & Pavón) Kosterm. is the only species with 4-thecous anthers in this otherwise 2-thecous genus.

Examples of species placed according to their staminal configuration despite obvious ties to species of a different genus are all Central American species currently placed in *Aiouea* (compare van

der Werff, 1987, 1988). In nearly all of its characters, including the wood structure, *A. costariensis* (Mez) Kosterm. is clearly a member of the *Ocotea insularis* group in the sense of Rohwer (1986). It is so close to *Ocotea skutchii* C. K. Allen as to make it very difficult to separate the two in fruit. *Aiouea lundelliana* C. K. Allen, a member of the same group, is even more obviously intermediate between the generic concepts in that its staminal configuration is variable within the same inflorescence (cf. van der Werff, 1984; Rohwer, 1986). In other Central American species of *Aiouea* the ties to a particular species or species group of *Ocotea* are not as clear, yet there is no doubt that they are closer to that genus than to the South American species of *Aiouea*.

In South America, *Aiouea* is very similar to species that used to be ascribed to the genus *Phoebe*. Again, the main difference is in the number of thecae, but it has long been known that in several of the "*Phoebe*" species only the outer anthers are 4-thecous, whereas the inner ones are 2-thecous. "*Phoebe*" is placed in quotation marks here because in the Neotropics it is anything but a good genus. The type of *Phoebe* is from Asia, and in all of the palaeotropical species the fruit is subtended by erect, enlarged, lignified tepals on a scarcely thickened pedicel, clasping the base of the fruit. Such a structure does not occur in any of the neotropical species. In some of them there are persistent tepals, but they are not enlarged, and either erect on the margin of a well-developed cupule or spreading from a swollen pedicel or a small, disklike cupule. Others have a normal, more or less bowl-shaped cupule, as in most species of *Ocotea*. Many of the neotropical species currently ascribed to *Phoebe*, in particular many Central American and Andean species, probably belong to *Cinnamomum*, as suggested by Kostermans (1961). However, transferring all of them indiscriminately to *Cinnamomum* seems rather precipitant. Some are clearly *Ocotea*, several may go to *Aiouea* after a revision of the generic delimitation, and still others may represent a genus of their own.

A third example of a probably polyphyletic genus in the New World is *Endlicheria*. It is defined by the combination of two characters, which indicate a common level of advancement rather than a common origin: (1) anthers 2-thecous, and (2) flowers unisexual. Some species of *Endlicheria* are extremely close to certain species of *Rhodostemonodaphne*. *Endlicheria metallica* Kosterm. and *R. grandis* (Mez) Rohwer can only be separated by counting the number of thecae per anther. It is questionable whether they should even be treated

as different species. Another striking similarity is found between *E. vinotincta* C. K. Allen and *R. celiana* (Allen) Rohwer. These two, although undoubtedly separate species, agree in many characters, from their reclining habit via their indument and the structure of their slender, pendent inflorescences to the development of peculiar, membranous, possibly glandular outgrowths of the filament on both sides below the anther. Especially this last-mentioned character makes it highly unlikely that the overall similarity is a mere convergence.

Other species of *Endlicheria*, e.g., *E. dysodantha* (Ruíz & Pavón) Mez and *E. pyriformis* (Nees) Mez, are much more similar to *Ocotea*, although they cannot be linked to a particular species. In *E. anomala* (Nees) Mez only the outer whorls are 2-theous, whereas the third whorl is 4-theous. Its fruit has a very small cupule that is lobed by the persistent bases of the tepals. Such a fruit structure is otherwise unknown in *Endlicheria*, but a rather similar form occurs in *Ocotea camphoromoea* Rohwer. This supports the view that *E. anomala* has been derived from *Ocotea* independently from other species of *Endlicheria*.

The *Endlicheria* species that form the core of subg. *Ampelodaphne* (*E. arunciflora* Mez, *E. bracteata* Mez, *E. glomerata* Mez, *E. macrophylla* (Meissn.) Mez, *E. multiflora* (Miq.) Mez, and *E. verticillata* Mez) need further investigation. With their crowded, nearly verticillate leaves and their numerous, minute flowers in profusely branched, bracteate inflorescences, they look not only unlike any other species of *Endlicheria*, but unlike any other neotropical Lauraceae at all. It is possible that they, too, have been derived from *Rhodostemonodaphne*, but independently from the species mentioned above. How the ancestral forms of this group may have looked is illustrated by *E. lorentensis* O. C. Schmidt, which has been described in *Endlicheria* despite its 4-theous anthers, based on its overall similarity to this genus.

All of the above cases suggest that the distinction between 2-theous and 4-theous anthers should be dropped for the purpose of generic delimitation. What would this mean for the system of the Lauraceae? Actually, the change would only be moderate. Some genera already comprise species with 2-theous and with 4-theous anthers (see above), and sometimes the number of thecae is variable within otherwise very homogeneous species (e.g., in *Urbanodendron verrucosum* (Nees) Mez, see Rohwer, 1988). In the New World only the three genera discussed above would need to be (partly) dismembered, and this would make the classifica-

tion more natural. On the other hand, it would become technically more difficult, but not impossible, to describe the difference between *Ocotea* and *Aniba*. In the Old World the change would involve only a few genera, but a large number of species. *Alseodaphne* and *Dehaasia*, with together some 80–90 species, would have to be merged, and new generic definitions would have to be found in the complex formed by *Lindera*, *Litsea*, and *Actinodaphne*, with together some 600–800 species. Within this complex the involucre enveloping whole or partial inflorescences is sometimes derived from bud scales at the base of the inflorescence and sometimes from floral bracts. There are also marked differences in the inflorescence structure (Kostermans, pers. comm.), which do not parallel the 2-theous/4-theous distinction, but which may correspond to structurally different groups in wood and bark characters (Richter, 1981). Only the sheer size of this complex precludes an effective revision. All other genera with 2-theous anthers, whether palaeotropical or neotropical, are either definable by additional floral or fruit characters, or their species had already been placed within a genus with 4-theous anthers by a previous author.

OTHER GENERIC CHARACTERS

But what about the value of other characters? Are they really more reliable than the number of thecae? The answer is more complicated than the question implies. No single character has exclusively one well-defined state in every genus. Somewhere in the family we always find characters not so clearly expressed, or intermediate states, or exceptions to the prevailing state of a genus. This statement, however, is only possible because we still can define genera, as groups with a syndrome of certain characters that are constant or nearly constant for this particular group, but may be variable in other groups defined by other characters. Staminodia, for example, are consistently absent in *Rhodostemonodaphne* and consistently large and glandular in *Persea*, but in *Ocotea* they can be absent, or small and nonglandular, or small with a glandular tip, or with a relatively large apical gland. This means that on the one hand any character will be misleading when given too much emphasis, and on the other hand any character (including the number of thecae) can be useful in conjunction with others.

Especially the fruit characters deserve more attention. With few exceptions (which need further investigation) they are remarkably constant within

natural groups as defined by other, often less obvious characters. Of course, the fruit characters are not diverse enough to differentiate all genera, but when they do show a clear-cut discontinuity, this mostly warrants a generic distinction. Unfortunately, nearly all conceivable intermediates are present in the large genus *Ocotea*, which is defined only negatively, i.e., by the absence of the diagnostic characters of more distinctive genera.

A good example of the variation of important characters (including fruit characters) within a genus is found in the neotropical species of *Persea*. In *Persea* subg. *Persea* the tepals are equal, widely patent to reflexed at anthesis, and lost in fruit, whereas in subg. *Eriodaphne* they are unequal, almost erect to slightly spreading at anthesis, and persistent, indurate, and widely patent in fruit. This seems to be a better distinction than found between many genera, but the gap is bridged by a few Central American species (*P. pallida*, *P. rigens*, *P. steyermarkii*, *P. sylvatica*), and by the Asian subg. (or genus) *Machilus*. These species have the equal tepals of subg. *Persea*, but they are persistent in fruit as in subg. *Eriodaphne* (although usually not incrassate in *Machilus*). Representatives of this group also occur in Venezuela, Ecuador, and Peru, but lack of good collections has hampered their correct placement. Recently, a *Persea* from Surinam was described with yet another combination of characters. Its tepals are unequal as in *Eriodaphne*, but deciduous, as in *Persea* (van der Werff, 1989).

The number of thecae is also variable in the neotropical *Persea* species. Most commonly one finds nine 4-celled stamens, but some species have nine 2-celled stamens, six 4-celled and three 2-celled stamens, or six 4-celled stamens and the third whorl staminodial. Needless to say, our understanding of this genus is far from complete, and it is equally not clear how to differentiate *Persea* from its closest relatives, especially in Asia.

While *Machilus* and *Phoebe* are clear-cut genera in Asia, the distinction between South American *Persea* subg. *Eriodaphne* and Asian *Phoebe* can be difficult. As mentioned above, the tepals are unequal and more or less patent in fruit in the former group, whereas in the latter they are (nearly) equal and erect. However, in some species of subg. *Eriodaphne* the "slightly unequal" tepals are less different from each other than the "nearly equal" tepals in some species of *Phoebe*, and in some species (e.g., *Persea cuneata* Meissn., see fig. 3 in Kopp, 1966) they can be nearly erect. If *P. cuneata* was an Old World species, it would be placed in *Phoebe* without much hesitation, or in

Apollonias, if this is kept separate from *Phoebe*, based on its 2-theous anthers.

What can we expect from future studies on neotropical Lauraceae? As more and better collections become available, the number of species will increase and the distribution of the taxa will become better known. Some of the new species will possess such unusual combinations of characters that additional genera will have to be described. Two genera have recently been described, *Williamodendron* (Kubitzki & Richter, 1987), initially only known from Amazonian Brazil, northern Colombia, and Costa Rica, but now also known from Peru and southern Brazil, and *Povedadaphne* (Burger, 1988), only known from Costa Rica. We have mentioned earlier several taxa that probably represent additional genera. We estimate that 25–35% of the neotropical species of Lauraceae have not yet been described, and even under optimum conditions, collecting plus descriptive studies would require at least a decade before an inventory of neotropical Lauraceae will be reasonably complete.

LITERATURE CITED

- AUBLET, F. 1775. *Histoire des plantes de la Guiane françoise*, Volume 2. Didot, London, Paris.
- BENTLEY, R. & H. TRIMEN. 1880. *Medicinal Plants*, Volume 3. J. & A. Churchill, London.
- BURGER, W. C. 1988. A new genus of Lauraceae from Costa Rica, with comments on problems of generic and specific delimitation within the family. *Brittonia* 40: 275–282.
- GREUTER, W. (editor). 1988. *International Code of Botanical Nomenclature*. Koeltz Scientific Books, Königstein.
- KOPP, L. 1966. A taxonomic revision of the genus *Persea* in the western hemisphere. *Mem. New York Bot. Gard.* 14: 1–117.
- KOSTERMANS, A. J. G. H. 1936. Lauraceae. In: A. Pulle (editor), *Flora of Surinam*, Volume 2. Koninklijke Vereeniging Indisch Instituut, Amsterdam.
- . 1957. Lauraceae. *Commun. Forest Res. Inst.* 57: 1–64.
- . 1961. The New World species of *Cinnamomum* Trew (Lauraceae). *Reinwardtia* 6: 17–24.
- , H. V. PINKLEY & W. L. STEARN. 1969. A new Amazonian arrow poison: *Ocotea venenosa*. *Bot. Mus. Leafl. Harvard Univ.* 22: 241–252.
- KUBITZKI, K. & H. G. RICHTER. 1987. *Williamodendron* Kubitzki & Richter, a new genus of neotropical Lauraceae. *Bot. Jahrb. Syst.* 109: 49–58.
- KURZ, H. 1982. Fortpflanzungsbiologie einiger Gattungen neotropischer Lauraceen und Revision der Gattung *Licaria* (Lauraceae). Ph.D. Dissertation, University of Hamburg.
- MELL, C. D. & W. D. BRUSH. 1913. *Greenheart*. U. S. Department of Agriculture, Forest Service, Circular 211.
- MEZ, C. 1889. Lauraceae Americanae. *Jahrb. Königl. Bot. Gart. Berlin* 5: 1–556.

-
- RICHTER, H. G. 1981. Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderbd. Naturwiss. Ver. Hamburg 5.
- . 1985. Wood and bark anatomy of Lauraceae, II, *Licaria*. IAWA Bulletin, n.s. 6: 187–199.
- ROHWER, J. G. 1986. Prodromus einer Monographie der Gattung *Ocotea* Aubl. (Lauraceae), sensu lato. Mitt. Inst. Allg. Bot. Hamburg 20: 3–278.
- . 1988. The genera *Dicypellium*, *Phyllostemonodaphne*, *Systemonodaphne* and *Urbanodendron* (Lauraceae). Bot. Jahrb. Syst. 110: 157–171.
- SANDWITH, N. Y. 1939. Scientific names of Greenheart and Balata. Trop. Woods 58: 24.
- WERFF, H. VAN DER. 1984. Notes on neotropical Lauraceae. Ann. Missouri Bot. Gard. 71: 1180–1183.
- . 1987. Six new species of neotropical Lauraceae. Ann. Missouri Bot. Gard. 74: 401–412.
- . 1988. Eight new species and one new combination of neotropical Lauraceae. Ann. Missouri Bot. Gard. 75: 402–419.
- . 1989. A new species of *Persea* (Lauraceae) from Surinam, with a discussion of its position within the genus. Ann. Missouri Bot. Gard. 76: 939–941.